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Mating and/or social system to explain territorial responses: a comment on Christensen and Radford

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Studies investigating territorial interactions often find on the first glance seemingly contradictory results, in some cases the response to neighboring groups is stronger than the response to strangers (nasty-neighbor effect), whereas in other cases the response towards strangers is stronger (dear-enemy effect). Christensen and Radford (2018) provide a comprehensive and much needed review of the different responses for species that collectively defend a territory and what the causes and consequences of these variations may be. In group-living species, not only the identity of the intruder varies but also the resident group living in the territory consists of various individuals that have potentially differing interests and motivations. Therefore, studying these interactions in the context of group-living species is especially interesting, but also highly challenging.

Strangers

Although the dichotomy between neighbors and strangers sounds convincing, in practice, much more complexity is to be expected. In the case of meerkats, for example, besides neighboring groups that have a similar group structure as the resident group, they can encounter stranger coalitions with hugely varying composition. These can be roving male coalitions, looking for extra matings, females that have been evicted from their natal group either alone or in groups, or males and females that grouped together to form a new group searching for territories (Clutton-Brock and Manser 2016). In group-living species, the diversity of these intruding groups is potentially much higher compared to solitary or pair bonded species.

The phenomena where both the intruding groups are diverse and the territory owner group consists different individuals with different interest, such as finding potential mates or defending their mates deserves more attention. Christensen and Radford (2018) in several places indicate this interest in the composition of the stranger group but we think it deserves special attention since in this situation the dynamics are expected to be truly different compared to neighbor–stranger response differences in solitary or paired territory owners.

Causes of response variation

The authors emphasize the context-dependent variation and within group variation as important factors determining response variation. Convincing empirical evidence exists for the effect of population density, seasonal changes as well as encounter locations as context-dependent factors explaining response variation. However, what is not considered is the mating and/or social system determining the social structure of group-living species and as a consequence the dispersal of group members (Willems et al. 2013; Clutton-Brock 2016), which are crucial determinants in territorial defense. We predict that the social structure and dispersal strategies, philopatry in females or males, will likely explain some of the neighbor–stranger response differences between species, as the characteristics of the different categories of intruders are directly determined by these factors. It will also bring in the role of relatedness of intruders, how they are tolerated or competed, as has recently been shown in African wild dogs (Jackson et al. 2017), and what underlying cognitive processes may be required.

Future directions

As a perspective for the future, Christensen and Radford (2018) identify three key areas of interest, first theoretical modeling, second physiological hormonal mechanisms, and last the influence of anthropogenic disturbances. As the authors point out the knowledge of the physiological underpinning of differential responses between neighbors and strangers is currently minimal even in solitary species. It is important to investigating this further, yet it might be more rewarding to first obtain a complete picture in the context of single individuals or pairs defending territories.

The last key point suggested to be investigated is how anthropogenic changes are going to change territorial interaction, for example, by changing population density and territory sizes through habitat loss and fragmentation or alternatively by signals or cues being masked by anthropogenic noise. For both these mechanisms, it needs to be carefully considered how the predictions on

territorial interactions are going to be fundamentally different from territorial interactions of nongroup-living species and therefore what the added value is of investigating these specifically. In addition, anthropogenic changes do not directly affect territorial interactions, but the context-dependent variation via the factors of population density or the signal transmission, i.e. the effectiveness of communication. Although anthropogenic changes are not the ultimate explanations for the variation in territorial responses, they provide the differences in context enabling to test predictions.

For the specific case of investigating neighbor–stranger response differences for groups collectively defending territories, we suggest to first get a more fundamental understanding of these interactions for groups. We propose that focusing on theoretical modeling in combination with observational and experimental studies might provide a solid framework to make predictions on when to expect the different defense strategies. This work should especially focus on the role different individuals (e.g. dominance status, sex, and age) within a group take in territorial advertisement (Jordan et al. 2010), as well as during and after interactions with either neighbors or strangers (Müller and Manser 2008) combined with the composition (floaters, rovers, evicted females) of stranger groups. Our predictions would be that the different stages of territorial defense, in regards to who invests most in advertising or shows the most aggressive behavior to which intruder category, correlate to a large extent (Gavrilets and Fortunato 2014). In addition, on the few studies available, the influence of the mating and/or social system, affecting the philopatry of females or males and therefore the group structure of the resident group as well as the intruders should be tested, as an ultimate factor explaining the neighbor–stranger response differences.

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The importance of understanding costs and benefits: a comment on Christensen and Radford

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We find the review of Christensen and Radford (2018) timely, and agree with much of the content. Given the highly common occurrence of territorial defense in the animal kingdom, understanding the causes and consequences of variation in behavioral responses during these interactions is paramount. There are 3 main points we would like to make based on Christensen and Radford's review. First, for group-living species, we absolutely agree that a greater consideration is needed of the different incentives for individual group members to participate in territory defense. Differences in age, sex, rank, and size are prevalent among group members and will affect their decision to (a) remain in the social group or disperse and (b) invest in potentially costly group behaviors, such as territory defense (Mirville 2018; Nelson-Flower et al. 2018). The factors influencing these decisions are fundamental to our understanding of how cooperation both evolves and is maintained (Shen et al. 2017).

Second, it is perhaps too common for behavioral ecologists to talk about "costs and benefits" without fully knowing what the costs and benefits are. For this reason, we are pleased to see Christensen and Radford (2018) bring up the issue of post-interaction behaviors. Can we truly understand the "cost" of an interaction without measuring the changes in intragroup behavior following an interaction? While some costs of interactions are immediate, such as loss of breeding partners, injury or even death, other costs are less obvious (such as the decrease in affiliative behaviors among group members (Mirville 2018, reviewed in Radford et al. 2016). The same principle applies to the measurable "benefits" of intergroup interactions. Although there are some clear benefits from intergroup interactions, including the acquisition of new resources, other benefits, such as assessment of future dispersal opportunities and long-term intergroup tolerance, are less obvious. It is highly unlikely that the effects of intergroup interactions are isolated to the interaction event. Intragroup behavior following the interaction, while researched in some species, has received relatively little attention in others (Radford et al. 2016). Post-interaction effects could include the breakdown of intragroup coalitions, and changing patterns of intragroup mate choice. Although there has been a recent increase in studies investigating post-interaction effects, these studies are dwarfed in number by those that study the dynamics of the interaction itself. We, therefore, emphasize the need to study pre- and post-interaction behavioral dynamics to better quantify the costs and benefits of intergroup interactions, and for how long such effects may last. In some species, these effects may last a long time. For example, the infanticidal behavior of extra-group male lions (*Panthera leo*) after defeating the resident lion/s on a territory can lead to considerable declines in female reproductive success (Packer and Pusey 1983). In other cases, the loss of group individuals following an interaction, either through dispersal, eviction, or death, can lead to a group-level Allee effect